ABSTRACT: Residual feed intake (RFI) is a measure of feed efficiency that is independent of level of production, such as size and growth rate in beef cattle, and thus is a useful new trait for studying the physiological mechanisms underlying variation in feed efficiency. Five major physiological processes are likely to contribute to variation in RFI, these being processes associated with intake of feed, digestion of feed, metabolism (anabolism and catabolism associated with and including variation in body composition), physical activity, and thermoregulation. Studies on Angus steers following divergent selection for RFI estimated that heat production from metabolic processes, body composition, and physical activity explained 73% of the variation in RFI. The proportions of variation in RFI that these processes explain are protein turnover, tissue metabolism and stress (37%); digestibility (10%); heat increment and fermentation (9%); physical activity (9%); body composition (5%); and feeding patterns (2%). Other studies in cattle and studies in poultry similarly found these processes to be important in explaining RFI. The physiological mechanisms identified so far are based on very few studies, some of which have small sample sizes. The genomic basis to variation in these physiological processes remains to be determined. The physiological mechanisms identified so far are based on very few studies, some of which have small sample sizes. The genomic basis to variation in these physiological processes remains to be determined. Early studies have shown many hundred genes to be associated with differences in RFI, perhaps in hindsight not surprising given the diversity of physiological processes involved. Further research is required to better understand the mechanisms responsible for the variation in RFI in target populations and to marry the physiological information with molecular genetics information that will become the basis for commercial tests for genetically superior animals.

Key words: body composition, efficiency, feed intake, net feed intake, residual feed intake, selection

INTRODUCTION

The concept of residual feed intake (RFI) was one of several indices for calculating feed efficiency of growing cattle used by Koch et al. (1963) that recognized that differences in both BW maintained and BW gain affected feed requirements. They suggested that feed intake could be adjusted for BW and BW gain, effectively partitioning feed intake into 2 components: 1) the feed intake expected for the given level of production; and 2) a residual portion. The residual portion of feed intake could be used to identify animals that deviate from their expected level of feed intake and was moderately heritable, with efficient animals having less (negative) RFI.

Because RFI is by definition phenotypically independent of the production traits used to calculate expected feed intake, it allows comparison between individuals differing in level of production during the measurement period. This independence of RFI from production has led some authors to suggest that RFI may represent inherent variation in basic metabolic processes. For example, genetic variation in maintenance energy requirement per kilogram of metabolic BW was closely associated with genetic variation in RFI in young Hereford bulls (Herd and Bishop, 2000). In an experiment with laying hens, variation in maintenance energy expenditure was shown to be a major contributor to variation in RFI between hens with similar egg mass production and BW (Luiting et al., 1991a).

There is considerable individual animal variation in feed intake above and below that expected or predicted on the basis of size and growth rate [e.g., mice (Archer et al., 1998), poultry (Byerly, 1941; Luiting and Urff, 1991), pigs (Foster et al., 1983; Gilbert et al., 2007;
Physiological basis for residual feed intake

Hoque et al., 2007), and cattle (Archer et al., 1999). There is also evidence for a genetic basis to this variation in efficiency across these species, with estimates for the heritability of RFI that range from low to moderate presented in the reports just aforementioned and in the reviews by Archer et al. (1999) and Pitchford (2004). Over the past decade there has been greatly increased interest in breeding to improve beef cattle feed efficiency (Archer et al., 1999; Herd et al., 2003; Arthur et al., 2004; Arthur and Herd, 2005). However, the biological basis of such variation is yet to be fully understood. Study of the underpinning biological processes can inform prediction of the consequence to the reduction in feed intake sought by breeding animals for less RFI.

**PHYSIOLOGICAL BASIS**

Residual feed intake measures whether an animal eats more or less feed than predicted by published feeding standards or by comparison with measured feed intakes of like-type animals (e.g., same breed, sex, age) eating the same feed. In the late 19th century, it was established that farm animals did indeed follow the physical laws of conservation of mass and energy. It follows that, apart from error in measurement of its component traits (e.g., feed intake, BW, BW gain, etc.), variation in RFI must be underpinned by measurable differences in biological processes.

In broad terms, there are likely to be at least 5 major processes by which variation in efficiency can arise (Herd et al., 2004). These are associated with variation in 1) intake of feed, 2) digestion of feed (and the associated energy costs), 3) metabolism (anabolism and catabolism associated with and including variation in body composition), 4) activity, and 5) thermoregulation.

**Feed Intake**

Variation in feed intake per se is associated with variation in maintenance requirements of ruminants. As feed intake increases, the amount of energy expended to digest the feed increases, in part because of an increase in size of the digestive organs and increase in energy expended within the tissues themselves. This heat increment of feeding (HIF) has been known for considerable time (for example, it was routinely measured by Kellner in the 1890s), and in ruminants is approximately 9% of ME intake (Standing Committee on Agriculture, 2000). Webster et al. (1975) measured the amount of energy expended in the gut of the sheep as a consequence of eating and estimated that it could account for about 40% of the total HIF. Webster et al. (1975) considered that the remainder was due to increased metabolism in peripheral tissues. Given that selection for RFI is associated with differences in intake, then those animals that eat less for the same performance could be expected to have less energy expended as HIF.

The rate of ingestion and duration of the meal have been reported as key factors in determining the energy cost of eating in cattle (Adam et al., 1984). A study of feeding patterns of Angus steers bred for high or low RFI (Richardson, 2003) reported a trend ($P < 0.10$) for the high-RFI steers to have faster decline in average daily feeding session times over their feed intake test and to spend more time eating early in the test compared with low-RFI steers. Spectral analysis of feeding patterns for another group of these Angus steers found that the high-RFI steers had more variable temporal patterns of feed intake early in the RFI-test period compared with low-RFI steers, which appeared to quickly settle into a regular feed-intake cycle (Dobos and Herd, 2008). Robinson and Oddy (2004) reported genetic variation in 3 feeding behavior traits of feedlot steers, that they had moderate heritabilities, and were positively correlated with RFI, such that greater RFI was associated with longer time feeding per day, more eating sessions per day, and faster rate of eating (g/min). Feeding time and number of eating sessions, but not eating rate, also had positive genetic correlations with RFI, indicating that effects of some genes for these feeding behaviors were common with their effect on RFI.

**Digestion**

It is known that as level of feed intake relative to maintenance increases, the digestion of feed (as measured by total tract disappearance) tends to decrease (Standing Committee on Agriculture, 2000). Over and above systematic variation due to amount of feed eaten, there is also genetic variation in total tract digestion of feed. In ewes from lines of sheep selected for and against weaning weight, the magnitude of the difference was about 2 percentage units of organic matter digestibility around a mean of 70% (Herd et al., 1993). From these same sheep selection lines, 16-mo-old rams from the high weaning weight line were found to have a greater digestibility by 4 percentage units compared with rams from the low weaning weight line when fed near ad libitum (Oddy, 1993). Richardson et al. (1996) found that young bulls and heifers phenotypically ranked low or high for RFI tended to differ in their ability to digest DM by about 1 percentage unit when tested on a pelleted ration with a calculated DM digestibility of 68%. This difference in DM digestibility accounted for 14% of the difference in intake between the 2 groups of cattle. Digestibility was correlated with RFI of cattle fed a high grain-content ration while in individual pens in an animal house, with the magnitude of the correlation ($r = 0.44$) indicating that differences in digestibility accounted for 19% of the phenotypic variation in RFI in the animal house. The direction of the correlation indicated that less RFI (greater efficiency) was associated with greater digestibility (Richardson and Herd, 2004). The difficulty in precisely measuring small differences in digestibility indicates caution in assigning variation
in digestion as a major factor in explaining differences in RFI in beef cattle. Studies on monogastrics indicate that differences in digestibility are not important sources of variation in RFI [chickens (Luiting et al., 1994), pigs (de Haer et al., 1993), and mice (Bunger et al., 1998)].

There is known to be variation in supply of AA due, in part, to variation in efficiency of microbial protein production in the rumen (Kahn et al., 2000) and appearance in the portal vein (Lush et al., 1991). Between line differences of 9% in microbial protein production per unit of feed intake, as measured by urinary allantoin excretion (Kahn et al., 2000), and of about 28% in appearance of AA in portal blood by direct measure (Lush et al., 1991) have been reported in sheep fed relative to BW at levels above maintenance. In dairy cows, there is evidence that selection for high milk yield is accompanied by improvement in digestion or absorption, or both, of dietary energy and protein (Adams and Belyea, 1987).

Together, these results indicate that differences in the processes of digestion and in substrate availability, at least in portal blood, do occur. They provide a possible mechanism to explain variation in efficiency of nutrient utilization, without the need to invoke variation in nutrient utilization per se.

**Body Composition and Metabolism**

The deposition of the same weight of lean tissue and fat has different energy costs. There is more variation in the efficiency of depositing lean gain than fat gain. Theoretical partial efficiencies of nutrient use for fat gain are in the range 70 to 95%, and for lean gain approximately 40 to 50%. However, there is more variation in efficiency of lean (protein) gain due to greater variation in protein turnover than in fat. Moreover, protein turnover varies to a much greater extent between organs than does fat turnover. Accordingly, any variation in composition of gain, and in composition of the body, can influence the apparent efficiency of nutrient utilization. Notwithstanding any within organ variation, there is considerable potential for variation in whole animal energy use, simply through differential organ growth. In the few cases where contribution of body composition to genetic variation in heat production or feed efficiency have been studied, it was found that variation in composition was small relative to variation in heat production (Herd et al., 2004). Results for beef steers divergently selected for RFI (Richardson et al., 2001) showed that chemical composition was correlated with genetic variation in RFI, with steer progeny of low-RFI parents having less whole-body chemical fat and more whole-body chemical protein than progeny of high-RFI parents. The differences in energy retained in the body accounted for only 5% of the difference in feed intake, with the remainder (95%) due to heat production.

Tissues of the splanchnic bed include the gastro-intestinal tract, liver, spleen, pancreas and mesenteric fat depots. Cumulatively these organs, together with the associated connective tissue and blood vessels, comprise approximately 15 to 20% of the total body mass in ruminants (Seal and Parker, 2000). Estimates of the total oxygen consumption attributed to the tissues of the whole splanchnic bed in ruminants range from 35 to 60% (Seal and Reynolds, 1993), and approximately 20% for the gastro-intestinal tract alone (Cant et al., 1996). Eisemann and Nienaber (1990) reported that portal drained viscera consumed 25.4% and liver consumed 20.5% of whole-body oxygen uptake in steers. In a slaughter experiment using cattle divergently selected for RFI, Richardson et al. (2001) concluded that the weight of the highly active tissues of the gastro-intestinal tract and internal organs were not related to genetic variation in RFI. These authors concluded that the difference in ME intake following a single generation of divergent selection for RFI was due to metabolic processes rather than to changes in body composition. Oxygen consumption by the portal drained viscera has been reported to be directly associated with feed intake in beef cattle (Huntington et al., 1988). Given the strong correlation between feed intake and RFI, it is possible there are associated decreases in oxygen consumption of these tissues following selection for improved (less) RFI.

Mitochondria produce approximately 90% of cellular energy, are numerous in metabolically active cells (e.g., liver, kidney, muscle, and brain cells) and contribute as much as 10% of the BW of adult humans and, presumably, a similar proportion of BW in many animals (Ojano-Dirain et al., 2007). Variation in aspects of the energetic efficiency of mitochondrial function has been shown to explain phenotypic differences in growth rate and feed efficiency in many farm animals. For example, for associations with G:F in poultry, see reviews by Ojano-Dirain et al. (2007) and Bottje and Carstens (2009). In beef steers, no difference in mitochondrial function was observed between animals that were phenotypically low or high for RFI, but the rate of mitochondrial respiration was increased in the low RFI (more efficient) steers and flux of electrons through the electron transport chain impaired in the high (low efficiency) animals (Kolath et al., 2006). Evidence for variation in mitochondrial function accompanying genetic differences in energetic efficiency is provided by McDonald and Nielsen (2008) from mice with mice divergently selected for heat loss.

Differences in metabolites reported by Richardson et al. (2004) are in agreement with the body composition results described above. Leptin concentration, typically associated with increased fatness in cattle (Ji et al., 1997; Chillard et al., 1998; Minton et al., 1998), was positively correlated with steer RFI, which was in line with the greater fatness of the less efficient steers. Urea, reported to be negatively related to protein con-
tent in bulls (Robinson et al., 1992), negatively related to lean growth (Cameron, 1992; Clarke et al., 1996), and positively related with backfat in sheep (Clarke et al., 1996), also was positively related to genetic and phenotypic measures of RFI in steers (Richardson et al., 2004). Creatinine, positively associated with muscle mass in sheep (Cameron, 1992; Clarke et al., 1996) and negatively associated with fat depth in sheep (Clarke et al., 1996), was negatively associated with steer RFI (Richardson et al., 2004), providing indirect evidence for greater lean proportion and less fat content of the more efficient steers measured in the slaughter experiment by Richardson et al. (2001). The magnitude and direction of genetic correlations for measures of body composition with RFI provide additional evidence on the size of the effect of genes that affect body composition and RFI. Arthur et al. (2001) found that subcutaneous fat depth measured over the 12th and 13th ribs and rump to have positive genetic correlations with RFI of 0.17 and 0.06 in beef weanling bulls and heifers. For yearling bulls from several beef breeds, Schenkel et al. (2004) reported genetic correlations between RFI with fatness traits of similar magnitude to those reported by Arthur et al. (2001), being $r = 0.16$ with scanned backfat thickness and $r = -0.02$ with scanned intramuscular fat percentage. So in these young cattle, whereas these measures of body fat had statistically significant correlations with genetic variation in RFI, the measures of body fat explained less than 5% of the variation in RFI. In young feedlot steers, Nkrumah et al. (2007) reported slightly stronger genetic correlations for phenotypic RFI with backfat thickness and marbling fat score, both for scanned measurements on the live animal ($r = 0.35$ and $r = 0.32$) and measurements on the carcass ($r = 0.33$ and 0.28). In older feedlot steers and heifers, Robinson and Oddy (2004) reported genetic correlations of 0.48 and 0.72 for 12th-13th rib and rump fat depths with RFI, and 0.22 for intramuscular fat percentage, evidence for a much stronger association between the effect of genes controlling these measures of fatness and their effect on RFI. In pigs, where attainment of moderate levels of fatness in the carcass is also required, a moderately strong and antagonistic genetic relationship for RFI with carcass backfat thickness ($r = 0.44$) was reported (Gilbert et al., 2007).

In chickens, there are variable reports as to the contribution of differences in body composition to the variation in RFI. Luiting (1990) summarized reported genetic and phenotypic correlations of body fat traits with RFI that ranged from -0.40 to 0.45. In a later paper, Luiting et al. (1991b) found that the low-RFI line contained 3.4% more fat than the high-RFI line. Across 4 selection experiments in poultry, Tixier-Boichard et al. (2002) observed less body fatness in the high RFI lines, that is, the opposite result to that observed in cattle and pigs. In mice, improved RFI was associated with a slight increase in fat postweaning and a decrease in fat at maturity (Archer et al., 1998). The results discuss previously indicate that the magnitude of the association between body composition and variation in RFI is influenced by age and stage of maturity of the test animals. It may be that performance tests on beef cattle and pigs usually involve growing animals for which protein synthesis is more efficient than fat deposition, whereas in the adult animal, maintenance requirements for protein are greater than for fat, favoring an association between increased fatness and less RFI more typical of results for poultry and mice recorded for RFI (Tixier-Boichard et al., 2002).

Variation in metabolism can affect heat production. Many of these processes contribute to the maintenance energy requirement of an animal. There are demonstrated differences in efficiency of energy use for maintenance between animals (reviewed by Archer et al., 1999) and there is evidence that maintenance energy requirement per unit metabolic BW was closely associated with genetic variation in RFI (Herd and Bishop, 2000). Protein turnover in living animals is an energetically expensive process, and variation in protein metabolism has been shown to accompany genetic selection for growth and other traits in domestic animals (reviewed by Oddy, 1999). There is genetic variation in energy utilization within a tissue. In sheep and cattle selected for and against growth rate, the amount of energy expended per unit mass of muscle varied between lines by approximately 20%. A significant part of this variation was shown to be due to differences in the relative rates of protein degradation and protein synthesis within the muscle (Oddy et al., 1995, 1998). Calpastatin, a specific inhibitor of the calcium activated protease calpain system, and thus protein degradation, has been reported to differ for cattle selected for efficiency of feed use (McDonagh et al., 2001). Richardson and Herd (2004) reported a greater concentration of total plasma protein and greater blood concentrations of urea and aspartate amino transferase (a marker of liver function indicative for greater levels of protein catabolism) in cattle with high RFI, compared with cattle with low RFI, which together provide evidence for greater protein turnover in high RFI cattle.

Changes in efficiency of conversion of feed to gain and in the rate of protein degradation in response to selection for growth and leanness have been observed in many species ranging from chickens (Pym, 1990; Tomas et al., 1991) to rainbow trout (McCarthy et al., 1994). For example, chickens from lines selected for lean gain, or increased efficiency of conversion of feed to gain, had decreased rates of fractional protein degradation than control line chickens (Pym, 1990). Moreover, (Tomas et al., 1991) found differences in fractional degradation rate were associated with differences in net efficiency of protein utilization. In this study, decreased rates of degradation gave rise to improved efficiency of protein gain.

Variation in stress response between animals that differ in RFI has been reported. For example, in beef steers, evidence for genetic associations for RFI with
plasma cortisol and several red and white blood cell variables, indicative of high-RFI (low efficiency) animals being more susceptible to stress, is presented by Richardson et al. (2004). In laying hens from lines following divergent selection on RFI, the more efficient hens displayed a significantly reduced corticosterone maximum response following an exogenous ACTH challenge, but the response that was sustained for longer than the low efficiency line hens (Luiting et al., 1994). In young crossbred rams, poor feed efficiency, measured as high RFI or high FCR, was phenotypically associated with greater concentrations of serum cortisol prechallenge and a greater elevation in serum cortisol following ACTH challenge (Knott et al., 2008). Given that the physiological responses to stress include an increase in metabolic rate and energy consumption coupled with increase in catabolic processes such as increased lipolysis and protein degradation (Knott et al., 2008), variation in stress response warrants further evaluation as a mechanism for difference in feed efficiency.

Concentration of IGF-I in plasma is genetically correlated with growth and carcass traits and feed efficiency in pigs and beef cattle (Moore et al., 2005). Within Australian Angus cattle data available to 2004, IGF-I concentration measured before or at weaning was found to have a genetic correlation with RFI of 0.57, indicating that many of the genes responsible for greater concentrations of IGF-I in blood were also associated with greater RFI (Moore et al., 2005). Re-analysis of the previous and new available data to 2007 allowed 2 RFI traits to be distinguished: RFI \textit{postweaning} for younger cattle, typically bulls and heifers tested between 8 and 12 mo of age; and RFI \textit{feedlot}, for steers, typically older than 12 mo of age and being feedlot-fed before slaughter (Johnston, 2007). The genetic correlation between these 2 RFI traits was 0.59, indicating that there are many genes in common for superior RFI \textit{postweaning} and RFI \textit{feedlot}. Plasma IGF-I concentration was found to have a genetic correlation of 0.17 with RFI \textit{postweaning} and -0.22 with RFI \textit{feedlot}, indicating that only a minor proportion of genes responsible for IGF-I concentration were also associated with variation in RFI \textit{postweaning}, and that they or another small proportion of genes had an association in opposite direction with RFI \textit{feedlot}. Two consequences of this discovery were, first, that the accuracy of using IGF-I concentration to predict breeding values for RFI was reduced and, second, that effects of many genes on RFI differed between postweaning and feedlot test data.

\textbf{Activity}

Variation in heat production, and thus energy available for maintenance and growth, also occurs as a result of differences in energy expenditure associated with activity. Studies on monogastric species reveal the potential importance of differences in activity to variation in RFI. For example, in pigs total daily feeding time and number of visits to a feeding station are positively correlated with RFI \((r = 0.64 \text{ and } 0.51, \text{ respectively}; \text{ de Haer et al., 1993})\). Activity contributes to a substantial proportion of the variation in RFI in chickens (Braastad and Katle, 1989; Katle, 1991; Luiting et al., 1991b). Luiting et al. (1991b) concluded that 80% of the genetic difference in RFI between lines of chickens divergent for RFI could be related to a difference in physical activity. In lines of mice divergently selected for heat loss, Mousel et al. (2001) showed that the high heat loss (low efficiency) mice were twice as active as the low heat loss (high efficiency) mice and that this difference in activity accounted for 36% of the difference in feed intake between the selection lines. In lines of mice divergently selected for food intake corrected for BW, Bunger et al. (1998) found mice in the high food intake (low efficiency) line to be 3 times more active than mice in the low feed intake (high efficiency) line.

Difference in activity can also be associated with variation in RFI in cattle. Richardson et al. (1999) reported a phenotypic correlation of 0.32 for RFI with daily pedometer count that would indicate that about 10% of the observed variation in RFI was explained by this measure of activity. Mechanisms associated with variation in activity include work involved in feeding, ruminating, and locomotion at various speeds. Herd et al. (2004) calculated the energy cost of these activities for high and low RFI selection-line bulls and heifers under standard test conditions to account for approximately 5% of the increased feed energy intake by high-RFI (low efficiency) selection-line cattle.

\textbf{Thermoregulation}

The principal route for energy loss in ruminants is evaporative heat loss [through heat exchange in the lungs and nasal turbinates (Blaxter, 1962)]. To a large extent, this is regulated by rate of respiration, yet the authors are not aware of any study of the relationship between respiration rate and RFI. Postural change and other adaptations such as wetting, seeking shelter, and huddling do not by themselves constitute a large proportion of variation in heat loss except in extreme situations.

Hens with less RFI reportedly have smaller nude body areas through which they could lose energy and were also slightly better feathered and less active (Luiting et al., 1994). Luiting et al. (1991b) had suggested earlier that each of these factors was likely to impinge on thermoregulation and suggested that this may be a contributing factor to variation in RFI in chickens. However, the large difference in body size between these species indicates that the contribution of thermoregulation to variation in energy expenditure could differ markedly.

\textbf{Evidence from Genomics}

In recent years, the advent of whole-genome association studies, based on proprietary chips able to test for
allelic variants in thousands of genes, have been used to find gene variants associated with variation in RFI and to identify possible biological pathways contributing to the observed variation. Barendse et al. (2007) conducted a whole-genome association study for RFI measured on feedlot cattle from 7 beef breeds in Australia. They found 161 SNP, representing 141 genetic regions of the bovine genome, providing evidence for association with RFI for multiple genes in a wide diversity of metabolic pathways that include all the processes described above. Sherman et al. (2008) report 6 SNP that have an effect on RFI in feedlot cattle in Canada. Not all these RFI SNP showed association with feed intake and FCR showing these SNP may be affecting the underlying biological mechanisms of feed efficiency beyond feed intake control and BW gain efficiency (Sherman et al., 2008).

In an experiment to identify genes differentially expressed between animals with high and low RFI cattle, Chen et al. (2008) reported results from a microarray experiment using liver biopsies from Angus bulls from the Trangie RFI selection lines. They found 181 probes were differentially expressed between the animals with high RFI and low RFI. They represented 163 unique genes, from which 7 gene networks were derived. Their functions included cellular growth and proliferation, protein synthesis, lipid metabolism, carbohydrate metabolism, cancer, drug metabolism, and small molecular biochemistry.

**Integration of Biological Mechanisms**

Experience with studies of animals from lines selected for other traits (e.g., growth rate and wool production) indicates that no single mechanism is likely to be primarily responsible for the associated change in phenotype (Oddy, 1999). For example, studies of replicated lines of mice selected for divergence in growth rate resulted in mice with similar divergence in the selected trait, but markedly different phenotype with respect to body composition, feed intake, metabolism, and activity (Falconer, 1973). There are a limited number of cases in farm animals where a single gene mutation has occurred that lead to marked phenotype differences. One such example is the mutation in the myostatin gene that causes the double-muscled phenotype in cattle (Grobet et al., 1997). In short, the expectation is that many mechanisms are associated with the RFI phenotype.

That many physiological mechanisms contribute to variation in RFI was shown in experiments on Angus steer progeny following a single generation of divergent selection for RFI (Richardson and Herd, 2004). Differences in energy retained in protein and fat accounted for only 5% of the difference in RFI following divergent selection. Differences in digestion contributed conservatively 10% and feeding patterns 2% to the variation in RFI. The HIF contributed 9% and activity contributed 10%. Indirect measures of protein turnover indicate that protein turnover, tissue metabolism, and stress response contributed to at least 37% of the variation in RFI. Approximately 27% of the difference in RFI was due to variation in other processes such as ion transport, not yet measured (Figure 1).

**SUMMARY AND CONCLUSIONS**

Basic to the computation of RFI is calculation of the expected feed intake by an animal based on a measure of its BW and an allowance for level or quantity of product output. Rarely is composition of the output considered, nor are differences in locomotion, disease status, immunocompetence, or other metabolic processes that use energy. It follows that if there is no allowance made for the energy requirements of these processes, the reduction in feed intake sought by selection for low RFI may compromise the capacity of an animal to sustain these functions. In practical terms, there is a need for improved understanding of the genetic and phenotypic relationships between feed intake and the components of production at different phases of the productive life of the animal to be able to effectively utilize RFI to optimally improve whole production system efficiency.

Given the many biological processes that appear to underpin variation in RFI, it can be anticipated that several correlated changes in other important production and fitness traits may result from selection for RFI. Indeed, it is indirect improvement in many of these traits that is sought through implementing a breeding program that includes selection for less RFI. Further research is required to better understand the mechanisms responsible for the variation in RFI in target populations and to marry the physiological information with molecular genetic information that will become the basis for commercial tests for genetically superior animals.
LITERATURE CITED


